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Home-range size and overlap within an introduced population of the Cuban Knight Anole, *Anolis equestris* (Squamata: Iguanidae)

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Abstract

Home-range size and overlap within an introduced population of the Cuban Knight Anole, *Anolis equestris* (Squamata: Iguanidae). Many studies have investigated the spatial relationships of terrestrial lizards, but arboreal species remain poorly studied because they are difficult to observe. The conventional view of home-range size and overlap among territorial, polygynous species of lizards is that: (1) male home ranges are larger than those of females; (2) male home ranges usually encompass, or substantially overlap, those of several females; and (3) male home-range overlap varies but often is minimal, but female home ranges frequently overlap extensively. However, the paucity of pertinent studies makes it difficult to generalize these patterns to arboreal lizards. We investigated home-range size and overlap in the arboreal Knight Anole, *Anolis equestris*, and compared our findings to published home-range data for 15 other species of *Anolis*. Using radiotelemetry and mark-recapture/resight techniques, we analyzed the home ranges of individuals from an introduced population of Knight Anoles in Miami, Florida. The home ranges of both sexes substantially overlapped those of the same- and different-sex individuals. In addition, male and female home ranges did not differ significantly, an unusual observation among lizard species. If one compares both male and female home ranges to those of other *Anolis* species, Knight Anoles have significantly larger home ranges, except for two species for which statistical comparisons were not possible. Our results suggest that home ranges and sex-specific spatial arrangements of canopy lizards may differ from those of more terrestrial species.

Keywords: Squamata, Iguanidae, *Anolis*, home range, spatial relationships.

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Resumo

Tamanho e sobreposição de áreas de vida em uma população introduzida do lagarto cubano *Anolis equestris* (Squamata: Iguanidae). Muitos estudos investigaram as relações espaciais entre lagartos terrestres, mas as espécies arborícolas permanecem pouco estudadas devido a dificuldades de observação. A visão convencional do tamanho e da sobreposição de áreas de vida entre espécies poligínicas territoriais de lagartos afirma que: (1) as áreas de vida dos machos são maiores que as das fêmeas; (2) geralmente abrangem, ou se sobrepõem substancialmente, as áreas de várias fêmeas; e (3) a sobreposição entre as áreas dos machos varia, mas frequentemente é minima, enquanto as áreas das fêmeas geralmente se sobrepõem extensamente. Contudo, a escassez de estudos pertinentes dificulta uma generalização desses padrões para lagartos arborícolas. Usando técnicas de radiotelemetria e de marcação e recaptura, estudamos o tamanho e a sobreposição das áreas de vida dos indivíduos de uma população do lagarto cubano *Anolis equestris* introduzida em Miami, Flórida, e comparamos nossos resultados com os dados disponíveis na literatura para outras 15 espécies de *Anolis*. Em ambos os sexos, as áreas de vida se sobrepõem substancialmente com as áreas tanto de indivíduos do mesmo sexo como de sexos diferentes. Além disso, não houve diferença significativa entre as áreas de vida de machos e fêmeas, uma observação incomum em lagartos. As áreas de vida de machos e fêmeas de *A. equestris* foram significativamente maiores que as das outras espécies analisadas, com exceção de duas espécies para as quais não foram possíveis comparações estatísticas. Nossos resultados sugerem que as áreas de vida e os arranjos espaciais específicos de cada sexo para lagartos do dossel podem diferir daqueles de espécies mais terrestres.

Palavras-chave: Squamata, Iguanidae, *Anolis*, área de vida, relações espaciais.

Introduction

Some general patterns of spatial relationships observed among territorial, polygynous lizard species are as follows: (1) male home ranges (HRs) are larger than those of females; (2) male HRs generally encompass, or substantially overlap, those of several females; and (3) HR overlap between males varies from essentially none to substantial overlap, depending on the species. In contrast, female HRs frequently overlap extensively (Rand 1967, Stamps 1977, 1983, Schoener and Schoener 1980, 1982, Hicks and Trivers 1983, Jenssen *et al*. 1995, Tokarz 1998, Perry and Garland 2002, Haenel *et al*. 2003, Calsbeek and Bonneaud 2008). Theory suggests that these HR sizes and spatial arrangements result from the energetic costs of differing reproductive strategies. Thus, male reproductive success primarily is limited by access to potential mates and their defense against male intruders, whereas female reproductive success primarily is limited by resource (e.g., food and nest site) availability (Rand 1967, Stamps 1977, Jenssen *et al*. 1995, Perry and Garland 2002).

Many iguanid species seem to conform to the conventional model, including anoles (Schoener and Schoener 1980, 1982, Stamps 1983, Tokarz 1998, Calsbeek and Bonneaud 2008). However, most species investigated have been terrestrial; there are few studies of canopy-dwelling species. The few studies that have been published (Dalrymple 1980, Schoener and Schoener 1982, Hicks and Trivers 1983, Losos *et al*. 1990, 1991, Reagan 1992) involved observations of natural history or species-specific spatial relationships. Therefore, it is unclear whether similar sex-specific spatial relationships prevail among arboreal lizards, because an arboreal existence may impose conditions that dictate different

spatial patterns. For example, the canopy has reduced visibility compared to the trunk or ground, given the presence of branches and leaves (Johnson *et al*. 2010). It has been proposed that habitat strongly influences foraging mode and that more open habitats favor sit-and-wait predators, whereas cluttered habitats tend to favor active foraging (Moremond 1979, Cooper 2007). Reduced visibility in the canopy may promote more active foraging and more active patrolling of territory for defense against intruders and mate location (Eason and Stamps 1992, 2001). These activities may lead to substantially different spatial relationships (e.g., larger HRs) within and between the sexes compared to terrestrial sit-and-wait predators (Eason and Stamps 1992). Active foragers often are reported to be non-territorial, as opposed to sit-and-wait foragers (Pianka and Vitt 2003), but active-foraging and sit-and-wait foraging modes represent extremes along a continuum (Perry and Garland 2002, Butler 2005, Cooper 2007). Canopy species may be more active foragers than terrestrial species, but still may be somewhat territorial. The sex-specific spatial relationships of canopy species might not fit those observed for terrestrial lizards because of the difficulty in navigating the cluttered canopy environment. It is not clear what impact canopy dwelling might have on sex-specific spatial relationships.

Species of *Anolis* provide an excellent model system with which to investigate alternate hypotheses of spatial relationships. They vary broadly in habitat use, moving from the ground to the canopy and everywhere in between (Williams 1972, Losos 2009). Despite the plethora of *Anolis* studies, little has been published on canopy-dwelling species, particularly in regard to their sex-specific spatial relationships. A few studies have investigated spatial relationships among arboreal anoles that specialize on small perches (e.g., *A. angusticeps*, Schoener and Schoener 1982; *A. stratulus*, Reagan 1992; *A. valencienni*, Hicks and Trivers 1983; these generally found that these species conform to the model of spatial relationships described above.

We investigated the home-range size and overlap of the Cuban Knight Anole, *Anolis equestris,* to determine if their spatial relationships also conformed to the traditional spatial relationship model. This species has been classified as a crown-giant ecomorph (Williams 1972). Most crown giants are large, cryptically green species that inhabit canopies and primarily locomote by walking (Moremond 1981, Losos *et al.* 1990). The introduced population in Miami–Dade County, Florida, is well established and seems healthy. Although the native and introduced habitats have not been compared rigorously, informal observation by biologists familiar with both (R. Glor, J.J. Kolbe, J.B. Losos, pers. comm.) suggests that the introduced habitat closely approximates the native Cuban environment. We conducted a mark-recapture/resight and radio telemetry study on this species to examine home-range size and overlap. We compared results for this species to those of others for which comparable data are available.

Materials and Methods

We studied *Anolis equestris* from 31 August 1998–17 August 1999 with additional observations conducted through 24 February 2001. The study area comprised three sections of the University of Miami campus in Coral Gables, Florida, USA, in the vicinity of the Gifford Arboretum (Figure 1). The combined area totals ~14,000 m^2. We created a virtual grid for the area by mapping the perimeter and all major landmarks (trees, trails, pond, parking lots, etc.) with the aid of a Trimble GPS unit (GeoXH handheld with Zephr antenna, GPServ, Inc., Deerfield Beach, FL, accuracy to 0.3 m^2 with Coast Guard correction). We then recorded positions for each capture, resight, and radio-telemetered individual with reference to our map.

We captured individuals opportunistically with noose poles or by hand, and recorded the time and position of capture. Each individual was marked with a unique combination of

colored beads attached to their backs, following the method of Fisher and Muth (1989). Sex, mass, and snout–vent length (SVL) were recorded for all captures, and all lizards were released at the point of their capture. Adult age or size has not been addressed in this species or any close relatives. We observed hatchings/juveniles on the ground, and all our captured individuals were orders of magnitude larger, and likely adults.

We developed a back-pack style transmitter system to radio-track individuals using a G3 two-stage transmitter with LiBR 2030 batteries or SM1 single-stage transmitters with Renata 357 batteries (AVM Instrument Company LTD, Livermore, CA). Each unit (transmitter plus battery) was coated two or three times with Plasti-Dip (PDI brand, PDE inc., P.O. Box 130, Circle Pines, MN 55014), painted green with tempura paint (American Glue Corporation, Taylor, MI 48180) to blend with the lizards, and sealed for water-tightness with quick drying epoxy (Devcon 2-ton Crystal Clear Epoxy, Devcon Consumer Products, Des Plaines, IL 60018). We imbedded 4-lb monofilament line in the epoxy, and tied the monofilament to harnesses constructed of 0.25-in. elastic (Stretch-Rite brand, Rhode Island Textile Company, Pawtucket, RI 02862) dyed green to blend with the lizards. The maximum weight of units plus harnesses were 6 g for two-stage transmitters and 4.5 g for single-stage transmitters; we made every effort to place the lightest units on individuals, so that no unit was greater than 5% of an individual's body weight. In preliminary tests, we placed these units on a few individuals to validate their utility and confirm that they neither harmed the lizards or impeded their natural behavior in their habitats. (We often saw pairs mating or interacting with the backpacks on and observed no ill effects.) Individuals were tracked using a hand-held Yagi 3-element antenna and a CE-12 receiver (Custom Electronics, Urbana, IL).

Mark-recapture/resight data were collected via opportunistic visual encounters or radio-tracking three to five times each week. We used these data to calculate home-range sizes by three methods: minimum convex polygon (MCP), and 50% and 95% adaptive kernels (Hooge and Eichenlaub 1997). The program CALHOME (Kie *et al*. 1996) was used to calculate home-range size.

Mean home-range sizes were compared between sexes of *Anolis equestris* and between *A. equestris* and other anole species (data drawn from the literature; Table 1) via Mann-Whitney U test to determine if a significant difference in home-range size exists between male and female *A. equestris* and if significant differences in home ranges are apparent between other anole species and *A. equestris*.

Results

We captured 89 individuals between February 1998 and September 1999 (adult males, adult females, and subadult/juvenile individuals of undetermined sex). Male *Anolis equestris* were

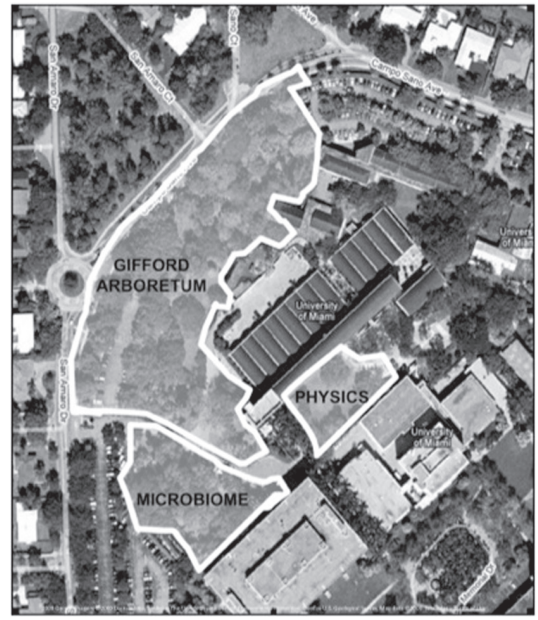

Figure 1. Study area. Cuban Knight Anoles were studied in three sections (termed here Gifford Arboretum, Physics, and Microbiome) of the University of Miami highlighted by white lines.

Table 1. Comparison of values for mean body size (SVL) and mean home-range sizes for species of *Anolis.* Snout–vent lengths are measured in millimeters and home-range sizes are in square meters. Home-range sizes from other studies were calculated as minimum-convex polygons. Statistical comparisons were made of male *Anolis equestris* HRs to those for males of other species, and female *A. equestris* HRs to those for females of other species via Mann-Whitney U test. Two species comparisons could not be made owing to lack of data, but of the remaining 13 species comparisons, 12 are statistically significant for both males and females, and the remainder (*A. smaragdinus)* was significant for males only. Ecomorph abbreviations as follows: CG = crown-giant, GB = grass-bush, TC = trunk-crown, TG = trunk-ground, TW = twig, — = unclassified. Source abbreviations are as follows: 1: Johnson (2007); 2: Losos *et al.* (1990); 3: Losos *et al.* (1991).

		Means			Means				
Species	**Eco-morph**	**Male SVL**	**Male HR**	***P*-value Male HR**	**Female SVL**	**Female HR**	***P*-value Female HR**	***N* (male, female)**	**Source**
A. equestris	CG	158.7	651.8	—	139.1	630.1	—	16, 11	
A. angusticeps	TW	48.2	4.53	0.0010	41.5	7.9	0.0003	22, 16	1
A. bahorucoensis	GB	44.6	9.42	0.0030	38.3	5.9	0.0001	15, 19	1
A. cristatellus	TG	58.5	29.4	0.0004	45.3	17.4	0.0001	22, 38	1
A. coelestinus	TC	65.3	17.6	0.0004	49.7	5.9	0.0001	27, 23	1
A. cuvieri	CG	130	325.8	—	N/A	N/A	—	1, 0	2
A. cybotes	TG	61.9	20.9	0.0001	51.0	10.8	0.0001	50, 35	1
A. frenatus	—	115.7	804.6	—	—	438.6	—	3, 5	3
A. grahami	TC	54.8	28.0	0.0001	44.7	27.6	0.0001	45, 37	1
A. gundlachi	TG	60.3	25.4	0.0001	44.5	18.6	0.0001	37, 42	1
A. krugi	GB	41.9	16.2	0.0002	38.0	22.0	0.0001	23, 39	1
A. lineatopus	TG	52.7	23.2	0.0001	43.4	8.4	0.0001	22, 45	1
A. olssoni	GB	43.8	14.6	0.0010	42.1	19.4	0.0006	18, 15	1
A. sagrei	TG	50.3	11.8	0.0007	38.3	5.8	0.0001	19, 18	1
A. smaragdinus	TC	56.6	21.9	0.0006	46.0	8.3	0.0043	20, 10	1
A. valencienni	TW	64.2	41.6	0.0012	59.0	69.3	0.0001	19, 33	1

larger than females in both mass and SVL (mass: $\bar{x}_{male}$ = 99.7g, range = 37 – 137g; $\bar{x}_{female}$ = 65.6 g, range = 35.8–88.5 g; SVL: $\bar{x}_{male}$ = 158.7 mm, range = 122–180 mm; $\bar{x}_{female}$ = 139.1 mm, range = 121–165 mm) and the difference between sexes was significant (mass: Mann-Whitney U = 7.38, $N = 41$, $P < 0.0001$; SVL: Mann-Whitney U = 6.70, $N = 31$, $P < 0.0001$).

Home ranges were calculated for 28 individuals (16 males, 11 females and 1 unconfirmed sex) for which five or more sightings were recorded (average number of sightings per

individual = 36; range = 5–120 with all but two having > 10 sightings). There is no significant difference in mean male and female HR sizes regardless of method used to calculate home-range size (Mann Whitney U test: MCP $P = 0.93$; 50% kernel $P = 0.33$; 95% kernel $P = 0.19$). However, the average size of male home ranges is consistently larger than the average female home range for all HR methods that we examined (male: 651.8 m^2 [MCP; SD = 749.44], 132.2 m^2 [50% kernel], 845.9 m^2 [95% kernel]; female: 630.1 m^2 [MCP; SD = 604.97], 86.6 m^2 [50% kernel], 542.4 m^2 [95% kernel]). All Mann-Whitney U calculations were Bonferroni corrected.

We restricted our analysis of spatial overlap to six pairs of individuals (two male pairs, and four male:female pairs) (Figure 2). Data for these individuals were collected during overlapping time periods and indicated HRs that overlapped spatially and temporally. (Some home ranges seemed to overlap in space, but may or may not overlap in time, because the data were collected at different times of the year. The six pairs mentioned here overlapped completely in time.) The degree of spatial overlap among all six overlapping pairs was either high or complete (75–99%). Other apparently overlapping pairs were not compared statistically because we did not collected data that allowed us to confirm their temporal overlap.

Statistical comparison of mean HR size of *Anolis equestris* by sex to other species yielded significant results for 13 of the 15 possible species comparisons (Table 1). Two species comparisons could not be made owing to lack of information, but it is unlikely that HRs of *A. equestris* would differ significant from those *A. cuvieri* or *A. frenatus*, both canopy-dwelling species with large home ranges. In contrast, species that typically live lower in the canopy or arboreal species with a very different body type from *A. equestris* (e.g., *A. angusticeps* and *A. valencienni*, both twig ecomorphs) differ significantly in home-range size (Table 1). HR differences remain significantly different when corrected for SVL (Wilcoxon Signed Rank Confidence Interval 0.2–0.55, $N = 13$, 95% confidence).

Discussion

The results of our study are consistent with the hypothesis that the HRs and sex-specific spatial arrangements of *Anolis equestris* differ from many less arboreal (i.e., non-canopy dwelling) anoles. We found no significant

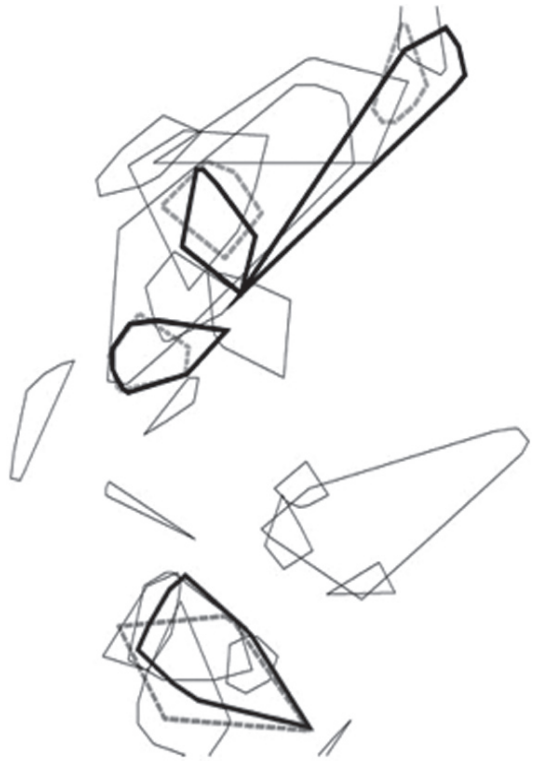

Figure 2. Home ranges of individual *Anolis equestris*. Depicted are the home-range areas calculated via the minimum convex polygon method. Home ranges of females (dotted gray lines) and males (black lines) that overlapped temporally and spatially. Home ranges indicated by thin gray lines are for individuals observed during this study, but data were collected at different times of the year (explained in text).

difference in the HR sizes of male and female *A. equestris*, a result that is unusual. However, consistent with the more traditional model, we found that HRs of female *A. equestris* overlapped substantially. Some HRs of male *A. equestris* overlapped nearly completely.

The similarity of HR sizes in male and female *Anolis equestris* may be the result of sample sizes and methodology, as well as a consequence of their combined energy requirements, habitat complexity, and resource distribution. *Anolis equestris* has been observed consuming nearly anything they can get in their mouths, including fruit, a wide range of insects (Brach 1976, Dalrymple 1980, Bels and Balthus 1988), birds, and other lizards. We observed one lizard consuming a migrating Blue-gray Gnatcatcher and others attempting to capture other anoles and a gecko, thereby confirming their omnivory. Habitat visibility may have a direct impact on multiple factors that leading to increased spatial overlap of males and females. The canopy at our study site was largely continuous, highly complex, and of low-range visibility, although visibility was not directly quantified. Studies have found that increased habitat complexity leads to lower competition and/or lower aggression in other species, in part as a result of visual isolation (brown trout: Höjesjö *et al.* 2004, Sundbaum and Näsland 1998; zebrafish: Basquill and Grant 1998). In *A. equestris*, lower aggression may lead to lower energetic costs for males, therby reducing differences in energetic requirements between the sexes and resulting in similarly sized habitats.

The apparent substantial HR overlap among both males and females, as well as between the sexes, may be an artifact of our methodology. Our HR estimations were made in two dimensions, but clearly, *Anolis equestris* lives and moves in three dimensions. If we could have calculated three-dimensional HR volumes, we might have found a very different pattern and perhaps a lack of, or decreased amount of, overlap. In other words, individuals very well may be territorial and not overlap much if HRs are examined in three dimensions. We could not collect data of this sort because of the exceedingly cryptic nature of *A. equestris* and the lack of canopy-reaching devices in our study area. A study by Reagan (1992) using canopy towers found that anole species distribute themselves vertically with respect to the distribution of their preferred perches. A similar examination of 3-D HRs in species such as *A. equestris* would be an extension of our study and a future direction that also would allow for further examination of the fit of *A. equestris* within the territoriality continuum.

Perhaps *Anolis equestris* and canopy species in general, do not fit the traditional dualities regarding foraging mode and territoriality—i.e., more terrestrial = more actively foraging vs. less territorial = more sit and wait foraging mode. Our study indicates that this introduced population of *A. equestris* may depart from the traditional model of sex-specific spatial relationships. Studies of native *A. equestris* and other canopy-dwelling species are required to determine if a general pattern exists for canopy species, and how possible patterns may correspond to foraging modes and territoriality. Application of novel technologies and field methodology within the canopy would undoubtedly further our understanding of a largely unknown microhabitat and its inhabitants.

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